Factors linking Pacific herring (*Clupea pallasi*) productivity and the spring plankton bloom in the Strait of Georgia, British Columbia, Canada

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ABSTRACT

The Pacific herring (*Clupea pallasi*) resource has supported one of the most important commercial fisheries on Canada's west coast for more than a century. Like many pelagic species, herring productivity has fluctuated throughout this period, especially for the largest population, which spawns in the Strait of Georgia. To provide long term sustainability and cogent management advice it is critical to understand the factors determining herring productivity. Since productivity can be influenced by survival of early life history stages, especially for pelagic species such as herring, we assessed the contribution of bottom-up forcing factors on young of the year (YOY) herring abundance and growth. Herring spawning is closely linked to the annual plankton production cycle and the match (or mismatch) between egg deposition and the initiation of the spring plankton bloom has a substantial impact on survival and production of YOY herring. Enhanced long-term monitoring of the production cycle could provide a better understanding and ultimately a prediction of Pacific herring production within the Strait of Georgia.

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1. Introduction

Pacific herring (*Clupea pallasi*) in the Strait of Georgia (SOG), British Columbia has supported important commercial fisheries for more than a century. During this time abundance has fluctuated markedly with periods of depletion in the 1930s and 1960s followed by rapid recoveries (Taylor, 1964; Ware, 1991). SOG herring also are an important forage species within this ecosystem transferring energy from lower trophic levels to the top predators (Ware and Thomson, 2005). Most SOG herring are migratory, entering SOG in the late autumn to overwinter and spawn (~March–April) after which they return to summer feeding grounds on shelf waters off the west coast of Vancouver Island (Taylor, 1964). This annual migration adds complexity to the determination of the energy contribution to the local SOG ecosystem. Hay and Fulton (1983) estimated the contribution of the released reproductive products to the SOG ecosystem as direct carbon input. Herring also contribute energy as prey for the myriad of fish, seabird and mammalian predators that converge on the annual spawning runs. Understanding the factors that affect Pacific herring survival and productivity will play a key role in understanding ecosystem processes and determine how best to move towards ecosystem-based management goals. Schweigert et al. (2009) present evidence that the abundance of herring at the end of their first summer within the SOG was a good predictor of the subsequent recruitment to the spawning population two and a half years later. The implication is that the factors determining survival up to the end of their first summer are critical to determining overall productivity of herring within the SOG. The goal of this study was to investigate some factors that could affect survival of herring from hatching in late March through to the autumn transition in late September. To this end we examined the following potential functional relationships: (1) the timing of the spring phytoplankton bloom and resulting year class strength; (2) September zooplankton abundance and juvenile herring survival and growth; (3) herring spawn timing and resulting juvenile growth and abundance. As per Cushing's (1975, 1990) match/mismatch hypothesis we noted that young of the year (YOY) herring survived better and grew larger during years when the timing of the mean annual spawning event most closely matched the timing of the annual phytoplankton bloom.

2. Materials and methods

2.1. Herring abundance

Estimates of the abundance of the sexually mature or spawning population of Pacific herring within the SOG were available from annual stock assessment catch at age model output (Martell et al., 2011). Input data consist of age composition, weight-

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at-age, total catch, and estimates of the egg deposition in each area. We determined the number of herring in the spawning population in each year for ages 2 through 10 and older.

The abundance of juvenile or YOY herring was determined from an annual small-mesh purse seine survey (Schweigert et al., 2009). The survey consisted of ten fixed transects, established at approximately equal intervals around the perimeter of the SOG and covering both open coastal areas and channels (Fig. 1). Each transect generally comprised 3–5 sampling stations spaced at 1 or 2 km intervals. Open-coast transects (1, 3, 5, 9, and 11) were established perpendicular to shore, with the first station lying about 600 m from the high-water mark, generally at 15-m depth. Transects 2, 4, 6, 8, and 10 were established across channels, with nearshore stations about 360 m from the high-water mark and also at 15-m depth. Each channel transect had a mid-channel station and, if possible, two stations on either side (Haegele, 1997). Most surveys occurred in mid to late September from 1992 to 2010, with each survey lasting about 2 weeks. No survey was conducted in 1995. During 1997–1999, only three stations were sampled on each transect (Haegele et al., 2005). Surveys were conducted in late September because YOY herring had grown sufficiently so that all were retained by the seine net and resulted in the lowest bycatch of small salmonids. September also was assumed to represent a point in the life history when much of the extensive early mortality had already occurred, and therefore this index was expected to represent a relative estimate of future recruitment to the population at age 3 (Barros and Toresen, 1998). A purse-seine (220 m long and 27 m deep, with marquisette webbing in the bunt to retain fish of standard length >3 cm) sampling an area of about 4000 m^2 was fished from three 11–12-m long vessels over the 18 year period.

The fishing techniques used (e.g. the velocity of pursing and drumming of the net) were kept as uniform as possible within and among cruises. All sets were conducted at night, beginning near dusk and continuing to completion of the transect. In general, one transect was completed each night (6–7 h), because of the travel time between transects and the available hours of darkness. Sampling at night takes advantage of the more homogeneous distribution of herring when feeding near the surface, whereas, during the day, YOY herring form discrete schools near the bottom (Blaxter, 1985). Catches were sorted by species and weighed, and samples of herring and salmonids were preserved in seawater formalin for further analysis in the laboratory. Catch weight of herring was determined by age group (YOY, age 1 and age 2+) as fish could be separated easily in the field based on length distribution. Except when catches were small and could be counted directly, the number caught by age group in each set was estimated by dividing the catch weight by the age specific mean weight in sub-samples taken from each set. A maximum of 200 fish per age group were examined per set for standard length (mm) and total weight (g) (Haegele, 1997). An earlier evaluation by Hay et al. (2003) compared both catch weight and numbers of YOY and age 1 herring in spring and autumn surveys as potential predictors of recruitment, and found no difference between weight and numbers. As a result, we used the estimated total weight (kg) of YOY captured in each set in our analyses. The estimated abundance of juvenile herring for each year was determined as the mean weight averaged over all stations. Nevertheless, there is significant variability in the data sets we used in the analyses. For example, the index of YOY abundance is the mean weight of YOY herring estimated for all sets made each year but in some sets the catch was very large so rapid
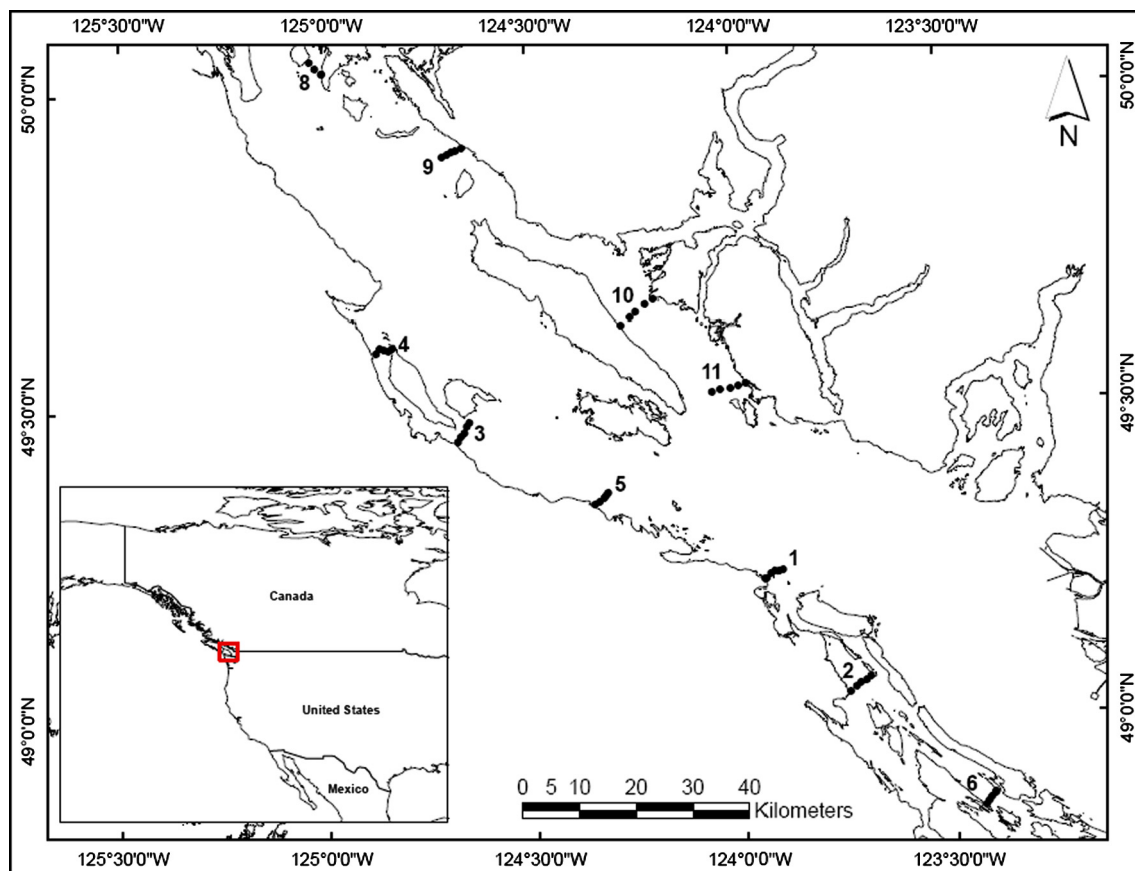

Fig. 1. Location of core transects for sampling YOY herring during purse seine surveys in the Strait of Georgia 1992–2010. Johnstone and Juan de Fuca Straits represent the northern and southern outlets, respectively.

on-board sampling was necessary. In these cases, the total catch was estimated as the number of totes of herring that were released from the net. The weight of herring in a tote was estimated from a single retained tote sub-sample. The resulting variability can be substantial. In some locations, the sets contained significant quantities of jellyfish that made sub-sampling and estimation of the proportion of YOY herring difficult and may affect the accuracy of the estimates.

2.2. Timing of herring spawning

Pacific herring spawning occurs over a protracted period usually beginning during the first week of March and frequently extending through the end of April (Hay et al., 2009). During these events, males release milt that discolors the water and provides a visible record of spawning locations. The locations, timing and extent of herring spawning have been documented since 1928 through either surface-based estimates or more recently SCUBA-based surveys (Hay and Kronlund, 1987). These records were used to determine the beginning, mid-point, end and duration of spawning for each year from 1992 through 2010. We determined the mid-point by arraying the day of the year (DOY) when spawning events occurred from earliest to latest and weighted them by the estimated shoreline length of the spawning bed (index of total egg deposition) observed on each day:

$$DSP_k = \frac{SL_t \cdot DOY_t}{\sum SL_t}$$

where DSP_k = day of the year when k proportion of the entire herring spawning occurred, SL_t = shoreline length of herring spawn observed on day t, DOY_t = day of the year when herring spawning occurred.

The 50th percentile was used as the mid-point date of the spawning for the year.

2.3. Timing of the spring bloom

The timing of the spring phytoplankton bloom, and its relationship with the subsequent production of zooplankton may be expected to have a significant impact on the feeding success and consequent survival and growth of newly hatched herring larvae. Determining the initiation of the spring phytoplankton bloom, however, is complicated because it appears that the blooms begin in localized segments of the SOG and subsequently spread throughout the entire area at varying rates depending on environmental conditions (Gower et al., 2013). Collins et al. (2009) and Allen and Wolfe (2013) developed a one-dimensional coupled biophysical model to predict the spring bloom date from wind speed, cloud fraction, and freshwater flux. We used the predicted annual spring bloom start dates for 1992–2010 from Allen and Wolfe (2013) in this analysis.

A second time series of spring bloom timing estimates was derived from satellite imagery. The chlorophyll a dataset was compiled from SeaWiFS level 3, 8-day composites, OC4v4 algorithm, processing version 2010.0. This dataset spans the period September 1997 to December 2010 at 9 km × 9 km spatial resolution. Since the spring of 2008, there have been significant gaps in the SeaWiFS dataset related to sensor aging. In order to bridge these gaps, MODIS Aqua data was used to supplement the chlorophyll time series (chlor_a product, OC3 algorithm, version 2009.1, with binning comparable to the SeaWiFS dataset). We observed an offset in the chlorophyll estimates from these two sensors (on average MODIS estimates were 1.7 mg m^{-3} higher than SeaWiFS, for 2008–2010 pixels in common from the Strait of Georgia); however

because the parameter of interest was timing, this offset was ignored.

For the SOG, the mean of all valid (cloud-free) chlorophyll values was extracted from pixels within the region defined by Ware and Thomson (2005) as British Columbia zone 3, for each 8-day period. Due to low sun angle at these latitudes, no winter chlorophyll estimates were available. The resulting time series that includes an amalgamation of SeaWiFS and MODIS data is shown in Fig. 2.

It is evident from the chlorophyll time series that, spatially averaged, the SOG does not display a classic large, single spring peak followed by lower biomass throughout the summer. Rather, phytoplankton production seems to occur as a series of brief bursts of variable magnitude throughout the spring, summer and autumn. For this reason we chose to estimate the initiation of the spring bloom, or more precisely, the initiation of the productive season, as either the first annual occurrence of two consecutive mean chlorophyll values greater than the annual median plus 5% (adapted from Siegel et al., 2003), or the first occurrence greater than a subjectively selected threshold of 6 mg m^{-3}. In the majority of years, the Siegel algorithm was used, but in 2009 there was a short-lived bloom preceding the Siegel date that was of sufficient magnitude (on average 19 mg m^{-3}) that we considered it to signify the beginning of the productive season. Similarly, in 2004 there was an early bloom (13 mg m^{-3}) that preceded the Siegel estimate by 2 weeks, which we considered to represent a more realistic start to the growing season (Fig. 2). We note that because the chlorophyll time series consists of 8-day composites, the temporal resolution of the bloom timing estimates also is 8 days. In addition, the possible confounding effect of the Fraser River plume on the optical chlorophyll estimates was assessed by examining daily and 8-day imagery from the period spanning spring bloom initiation in each year, and making comparisons between the distributions of chlorophyll and water-leaving radiance at 555 nm (nLw555, a proxy for turbidity) from SeaWiFS, MODIS and MERIS. In general blooms were spatially distinct from or broader in extent than the turbid region associated with the Fraser plume lending confidence that our timing estimates were valid.

2.4. Zooplankton abundance

Monitoring of zooplankton abundance in SOG is limited. Stepped oblique net tows to 20 m depth were conducted in conjunction with the juvenile herring surveys (Haegele, 1997). Other zooplankton sampling has been conducted opportunistically as part of ongoing monitoring of the physical and biological oceanography of the SOG (Li et al., 2013). Dr. David Mackas (Fisheries & Oceans Canada, Institute of Ocean Sciences, Sidney, BC, 2011, pers. comm.) compiled and summarized available zooplankton data including observations generated from the YOY herring surveys and provided these data for our analysis (Mackas et al., 2013). The data consist of the logarithmic transformed biomass of zooplankton in g m^{-2} for combined juvenile and adult Euphausia pacifica and adults alone, medium copepods (1–3 mm), large copepods (3–5 mm), Gammarid and Hyeriid amphipods.

2.5. Statistical analysis

Linear regression models were used to investigate the relationship between plankton abundance and survival and growth. Lowess smoothers were applied to describe non-linear relationships between spring bloom timing and herring spawning events and subsequent survival of YOY herring (Jacoby, 2000).
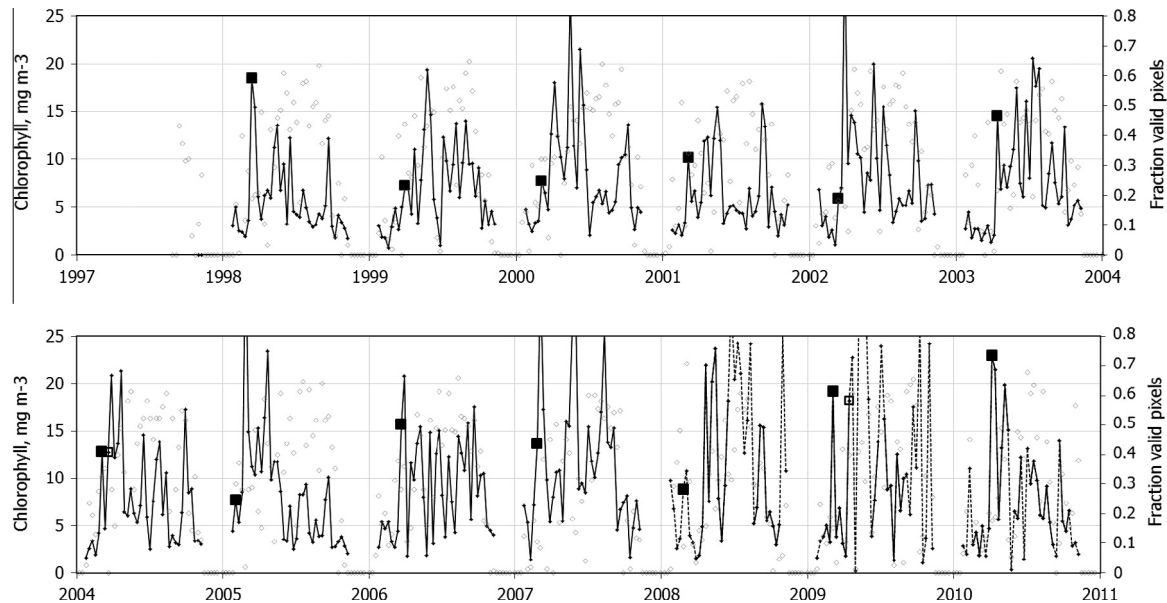
Fig. 2. Chlorophyll *a* estimates from 8-day composite SeaWiFS level 3 satellite images for the Strait of Georgia from 1997 to 2010, showing spring bloom timing estimates (black squares). Dashed lines are MODIS chlorophyll; grey symbols show the fraction of valid (cloud-free) Strait of Georgia pixels averaged to generate each estimate. Open squares represent Siegel algorithm estimates of spring bloom timing that were replaced by alternate estimates in 2004 and 2009 (see text for details).
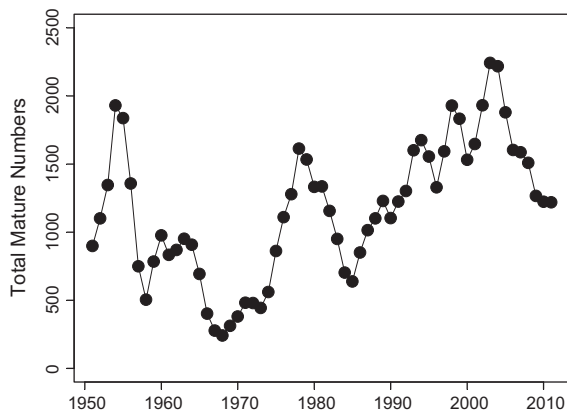

Fig. 3. Estimated Pacific herring adult abundance (millions) in the Strait of Georgia from 1951 to 2011.

Fig. 4. Index of young of the year (YOY) herring abundance from purse seine net surveys in the Strait of Georgia in the autumn from 1992 to 2010.

3. Results

Abundance of the adult herring population has fluctuated widely over the last half century with high abundance during the 1950s was followed by a population collapse in the late 1960s, after which the fishery was briefly closed (Fig. 3). Abundance increased rapidly through the 1970s following the fishery closure but declined again to low levels in the mid-1980s. Subsequently abundance increased dramatically to the recent historical high in 2003 and then declined again through to 2010. The substantial variation in adult abundance provides significant contrast for assessing survival during the pre-recruit life history.

The estimated YOY herring abundance from annual purse seine surveys similarly demonstrates substantial inter-annual variation with alternating strong and weak year-classes, but with a declining trend in the largest year-classes since 1998 (Fig. 4). The weakest year-classes appear to be those of 1992, 1993, 2005 and 2007.

The estimate of the date of initiation of the spring bloom from the wind driven model (Allen and Wolfe, 2013) and that from satellite imagery both indicate that the spring phytoplankton
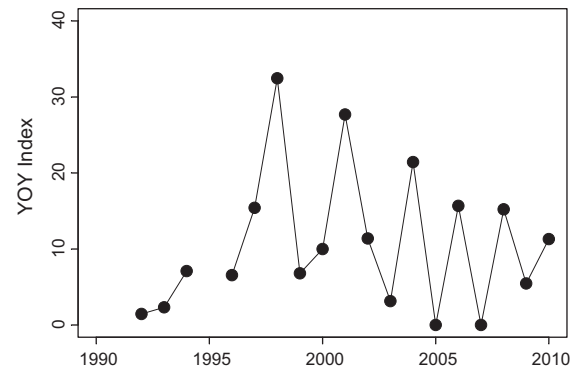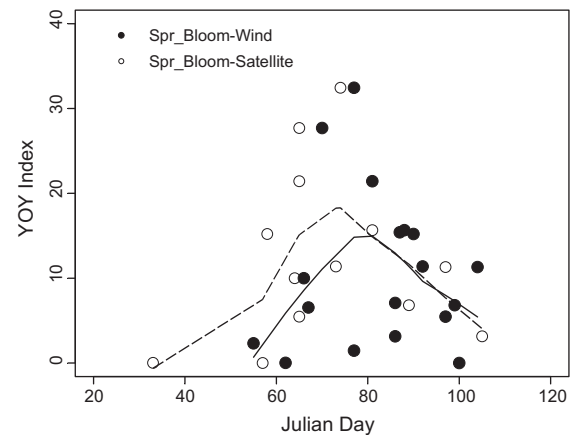

Fig. 5. Relationship between the abundance index of young of the year (YOY) herring and the estimated date of the spring bloom from the wind mixing model (Allen and Wolfe, 2013) or estimated from satellite imagery for the Strait of Georgia from 1992 to 2010. Lowess smooth fits to the data are also shown (wind – dashed, satellite – solid).

bloom occurs between DOY 60 and 100, although the satellite-based estimates suggest an earlier initiation of the spring bloom relative to the wind driven model (Fig. 5). Satellite-based estimates indicate most blooms occur between DOY 60 and day 80 with the majority around day 60. Both time series also indicate that the largest herring year-classes occur when the spring bloom begins between DOY 60 and 80 of the current year.

The importance of the date of the spring bloom not withstanding, we also hypothesized that the quantity of food available to YOY herring could be a factor in determining their survival to the end of the summer. The relationship between YOY herring abundance at the end of September and the estimated abundance of zooplankton in the SOG each year was investigated using linear regression, but no significant positive relationships existed for either the total weight of zooplankton or any of the six groups except *Gammarid* amphipods ($P < 0.05$).

While food availability, especially amphipod abundance, appears to play a role in YOY herring survival other factors also may be important. The timing of spawning in relation to the spring bloom should play a role in herring survival as per the match/mismatch hypothesis (Cushing, 1990). Although herring spawning generally begins around the first week of March, the start date of spawning does not appear to be strongly related to the abundance of YOY fish at the end of the summer (Fig. 6). Similarly, the mid-date of the spawning run is not strongly correlated with survival to the end of the summer. Interestingly, both the end date of the spawning period and the duration of the spawning period suggest a stronger link to survival and abundance of YOY herring at the end of September although with substantial variation (Fig. 6). Stronger year-classes are most frequent when spawning extends to or past the end of March (about DOY 90). The strongest year-classes also occur when the duration of the spawning period is about 25–30 days after which weaker year-classes are likely. Both of these observations suggest that the timing and duration of spawning and its link to the spring bloom timing are factors in determining the survival of young herring.

Linkage between the initiation of the spring bloom and spawn timing is illustrated by plots of the abundance of the YOY herring versus the difference between the estimated date of beginning of the spring bloom and the beginning, mid-point and end dates of the herring spawning period (Fig. 7). The relationship for all three metrics is variable but indicates that the strongest year-classes occur in years when the spawning period begins 1–2 weeks prior to the initiation of the spring bloom. It also appears that survival is
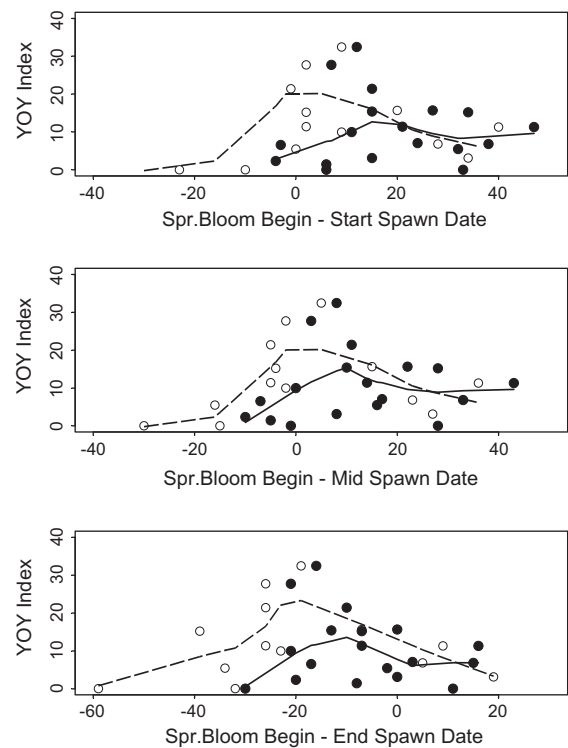

Fig. 7. Relationship between the index of young of the year (YOY) herring abundance and the difference between the beginning of the spring bloom and the start, middle or end-date of the spawning period from 1992 to 2010. Lowess smooth fits to the data are also shown (wind – dashed line, open circles, satellite – solid line, closed circles).

greatest when the spawning period ends no more than 2–3 weeks after the initiation of the spring bloom (Fig. 7).

A number of studies have suggested that the size of herring at the end of their first growing season determines their ability to survive the first winter (Paul and Paul, 1998; Foy and Paul, 1999). The weight of YOY herring shows an increasing trend from 1992 through 2006 with the exception of the 1996 and 2005 year-classes (Fig. 8). However, we found no relationship between the abundance of YOY herring in September (index of survival) and their average weight. However, there was a significant negative
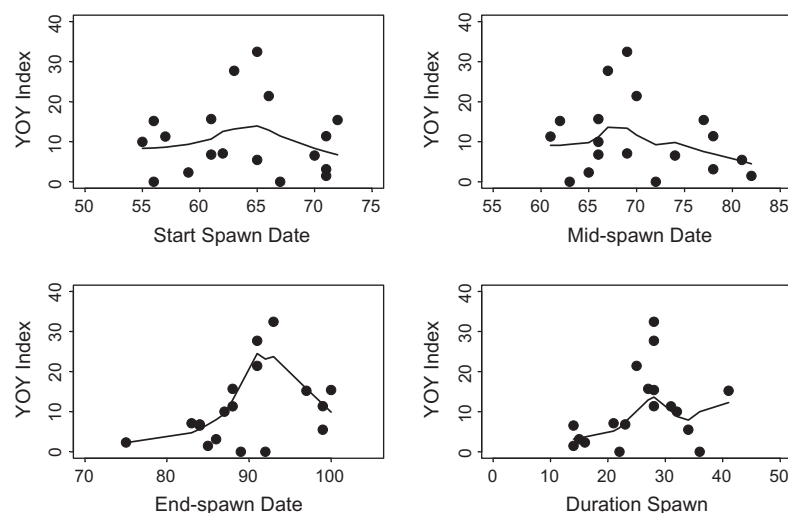

Fig. 6. Relationship between the index of young of the year (YOY) herring abundance and the timing of the spawning period from 1992 to 2010.
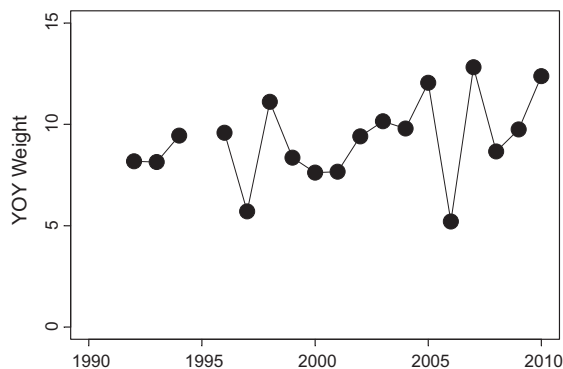
Fig. 8. Estimated average weight (g) of young of the year (YOY) herring in the Strait of Georgia from autumn purse seine surveys during 1992 to 2010.

relationship ($p = 0.076$) between the weight of YOY herring and the abundance of the recruiting year-class of age 3 fish 2 years later (Fig. 9) supporting earlier studies purporting that size during the first winter affects subsequent survival. There was no relationship between the average weight of herring in the autumn and the abundance of zooplankton at that time.

Finally, we investigated the relationship between juvenile herring weight and the timing of the spring bloom. The mean weight of YOY herring was not related to the timing of the spring bloom or the difference between the timing of the initiation of the spring bloom and the beginning, mid-point and end of the spawning period. It appears that growth conditions and survival of YOY year herring are mediated by different factors or by effects that occur at different times during the first year of life.

4. Discussion

SOG herring have experienced alternating periods of extreme abundance and scarcity during the past century (Ware, 1991; Fig. 3). Schweigert et al. (2010) investigated top-down and bottom-up forcing factors on the west coast of Vancouver Island herring population but were unable to establish which effects were most important in determining overall production. Earlier studies suggested that bottom-up forcing was important in determining long-term production trends for Pacific herring (Ware and Thomson, 2005; Perry and Schweigert, 2008). Other studies suggested that predation is a significant driver of herring population abun-
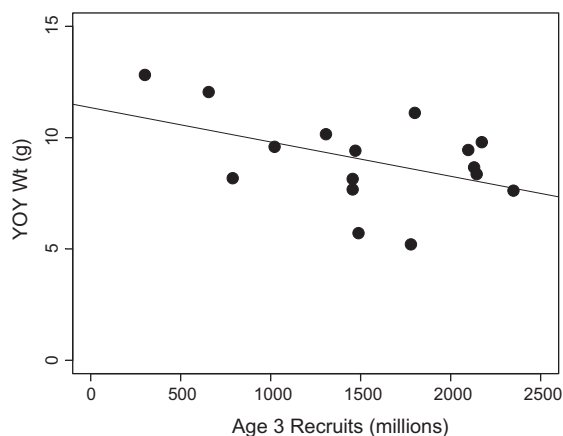

Fig. 9. Estimated average weight (g) of young of the year (YOY) herring in the Strait of Georgia and the subsequent abundance of age 3 recruiting fish for the 1992–2008 year-classes. No survey occurred in 1995.

dance. For example, Ware and McFarlane (1995) found that predation by Pacific hake was a significant predictor of mortality of pre-adult herring on the west coast of Vancouver Island. Similar results have been observed in studies of Atlantic herring (*Clupea harengus*). In the Barents Sea, Barros and Toresen (1998) found that abundance of cod (a main predator on Atlantic herring) and availability of capelin (as alternative prey) could influence juvenile herring survival. Other studies on Atlantic herring related juvenile survival to sea surface temperature and other oceanographic factors, but the relative importance of top-down or bottom-up forcing remains unclear (Fiksen and Slotte, 2002; Sætre et al., 2002). However, Schweigert et al. (2009) show that recruitment at age 3 for the SOG herring population was significantly related to the abundance of YOY herring at the end of their first summer. This suggests that factors determining early survival of young herring may be critical determinants of year-class size and recruitment to the adult spawning population. Sætre et al. (2002) and Axenrot and Hansson (2003) also found that a cohort that is weak at an early stage is unlikely to develop into a strong cohort later. Thus, external factors such as predation could have limited impacts on recruitment once juveniles have migrated offshore.

By focusing our study on the first 6 months of life we were able to investigate bottom-up effects between Pacific herring spawning time, timing of the spring plankton bloom and subsequent herring growth and survival in more detail. The available data suggest a linkage between the timing of the spawning period and the timing of the plankton production cycle as proposed in the match/mismatch hypothesis (Cushing, 1990). The timing of herring spawning in the SOG has been thoroughly documented but explanations for annual variability are lacking although there are indications of a link to the tidal cycle (Hay, 1990) and water temperature (Ware and Tanasichuk, 1989). Herring generally initiate spawning in one or more locations where it continues for a matter of days then ceases at that site. Subsequently, it may begin in another location within the SOG or it may stop entirely for a matter of days before resuming at that or another location (Hay 1985; Hay and Kronlund, 1987). As a result there may be gaps in the timing and extent of spawning. There also may be some minor errors in the reporting of the start date of spawning at particular locations due to limited reconnaissance, poor weather, and uncertainty in the location of the spawning. Nevertheless, we estimated the beginning and end of the spawning period as the dates of the first and last spawning events. The mid-point or peak of spawning was estimated as the weighted average of the array of spawning dates based on the estimated linear length of the egg bed at that location on that day. Any errors in these dates should be minor.

Somewhat greater uncertainty exists around the timing of the spring bloom both from the wind-driven model (Yin et al., 1997; Collins et al. 2009; Allen and Wolfe, 2013) and the satellite estimated bloom dates (Fig. 2), so both were considered. Variability in wind intensity and timing of the Fraser River freshet during the spring can affect the predictions from the wind-driven model while the accuracy of the satellite estimates is constrained by the 8 day window of available chlorophyll data. Gower et al. (2013) also noted that the phytoplankton bloom may be initiated or seeded in a small part of the SOG before becoming widespread. Thus, there are spatial and temporal fluxes in the progression of the bloom that can introduce error into the estimate of the date of bloom initiation. Nevertheless, the relationship between the abundance of YOY herring and the onset of the spring bloom (Fig. 5) while variable suggests that there is an optimal survival window. The earliest and latest bloom initiation dates resulted in smaller herring year-classes while intermediate dates resulted in the largest year-classes.

Although the timing of the start of the spring bloom appears important it must be followed by sustained production of plankton

(Fig. 2) to support the continued growth and survival of YOY herring. Unfortunately, the sampling of the plankton community is intermittent and sparse and the available index of zooplankton biomass is a composite of the available data. The sampling is not necessarily systematic or representative of the entire SOG and it is very unlikely that the point sampling in autumn was indicative of the production throughout the summer. The diets of juvenile herring during the summer consist largely of large and small copepods, fish eggs, larvaceans, juvenile euphausiids and mysids in Prince William Sound, Alaska (Cooney et al., 2001). Later in autumn benthic amphipods and polychaetes became prominent diet items. The indices of plankton biomass anomalies in the present study do indicate positive covariation between YOY abundance and food supply (not shown) although the only statistically significant relationship occurred for *Gammarids*.

The other important component of match/mismatch between YOY herring and food supply relates to the timing of the spawning period (Fig. 6). We found no clear relationship between the abundance of YOY herring and either the start date of the spawning period or the mid-date alone but the timing of spawning in relation to the timing of the phytoplankton bloom is important (Fig. 7). It also appears that the largest year-classes of herring resulted when the last spawning occurred by about DOY 90 or roughly the end of March. The duration of the spawning period also appears important because the strongest year-classes resulted from a spawning period that extended over about 25–30 days. In years when the spawning period is of short duration, the match of hatching with initiation of the spring bloom must be more closely aligned to ensure good survival and the probability of this occurring over multiple years is likely very low. More often spawning needs to be spread out in time to take advantage of the pulses in plankton production (Fig. 2) that occur in time and space as waves of herring larvae hatch from the various spawning events. Given the roughly 2 week incubation period of the herring eggs, the timing of the hatch would correspond well with a widely distributed plankton bloom throughout the SOG (Gower et al., 2013) and presumably a ready food supply for the newly hatched larvae.

The other aspect of herring production is growth in biomass of YOY herring. There is an indication of an increasing trend in average weight over time (Fig. 9) with the exception of 1996 and 2005. It is clear that 2005 was an anomalous ocean year (Crawford and Irvine, 2011) but 1996 may have been negatively affected by the early stages of the very strong 1997–1998 El Nino. There were no significant relationships between mean weight of herring and plankton indices collected in the autumn but these are unlikely to reflect the entire annual plankton production. The average weight of YOY herring in September was not related to the YOY abundance index. However, the average weight of YOY herring was significantly negatively related to the abundance of the year-class as determined at maturity at age 3 (Fig. 9). It suggests that food supply may be less limiting during the first summer but becomes more limiting once fish migrate out of the SOG to offshore feeding areas. It would be consistent with density dependent growth as noted previously by Tanasichuk (1997) for the west coast of Vancouver Island herring stock. Herring that are part of a large cohort compete more for food and so tend to grow more slowly than those in weaker cohorts where food may be more plentiful, as demonstrated for the strong 1977 year-class that occurred widely throughout the northeast Pacific (Hay et al., 2001).

The timing of the spawning period in relation to the spring bloom does not appear to play a significant role in the growth of YOY herring. Positive but non-significant co-variation exists between autumn YOY herring weight and the difference between the initiation of the spring bloom and the beginning, mid-point, or end of the spawning period based on the satellite data. It is evident from Fig. 2 that there can be substantial inter-annual variation in the plankton bloom over the course of the year. Hence, although timing of the bloom and herring spawning may appear optimal available food supply may vary from year to year affecting subsequent growth but not necessarily survival.

The focus of this study has been on bottom-up processes that may affect YOY herring abundance and growth. The available data provide support for a linkage between herring spawn timing and the associated spring phytoplankton bloom and subsequent herring survival. A better understanding of the progression of the annual plankton cycle in time and space could improve the statistical description of this relationship. In addition, there are top down forcing factors on the herring population that require investigation to more fully understand potential limitations on herring productivity.

5. Conclusions

The survival of YOY herring from hatching to the end of their first summer within the SOG is a function of the timing of the annual herring spawning cycle and the onset of the spring plankton bloom. Years in which the herring spawning period began about 1–2 weeks prior to the initiation of the spring bloom and ended 2–3 weeks after the beginning of the spring bloom usually resulted in the highest abundance of herring during September surveys. The mean weight of YOY herring was inversely related to the abundance of YOY herring at the time of recruitment to the adult population but not during the first summer suggesting that density-dependent effects may be manifested more strongly after migration out of the SOG. The results are consistent with Cushing's (1990) match/mismatch hypothesis.

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